Wilson Bull., 114(4), 2002, pp. 474–478

SEASONAL VARIATION IN SEX RATIO OF FLEDGLING AMERICAN KESTRELS: A LONG TERM STUDY

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ABSTRACT.—The Early Bird Hypothesis predicts that males fledged early in the breeding season have an advantage over their later-fledged counterparts during competition for breeding sites. We tested this hypothesis by examining the sex ratio of 1,025 fledglings from 265 broods of American Kestrels (*Falco sparverius*) breeding in nest boxes in Wisconsin during the period 1968–1997. We found a seasonal shift in the sex ratio: the sex ratio of fledglings was biased toward males early in the breeding season, but became increasingly biased toward females as the season progressed. Our results provide support for the Early Bird Hypothesis and suggest that the steepness of this trend may decrease with increasing latitude. *Received 10 December 2001, accepted 5 July 2002.*

The offspring sex ratio in most species of birds rarely differs from parity (Clutton-Brock 1986, Koenig and Dickinson 1996). Nonetheless, recent studies have documented many exceptions from parity (Gowaty 1993, Ellegren et al. 1996, Svensson and Nilsson 1996, Komdeur 1996). In particular, several species of raptors showed a seasonal shift in the sex ratio, although the total annual number of male and female offspring was equal. In the Eurasian Kestrel (*Falco tinnunculus*; Dijkstra et al. 1990, Daan et al. 1996) and Lesser Kestrel (*Falco naumanni*; Tella et al. 1996) the fledgling sex ratio was skewed toward males early in the season while late broods had an excess of females. Recently the same seasonal trend was found in a Florida population of the American Kestrel (*Falco sparverius*; Smallwood and Smallwood 1998), but not in a Canadian population of the same species (Wiebe and Bortolotti 1992, and see Smallwood and Smallwood 1998). Differential parental investment (Trivers and Willard 1973), local competition for resources between parent and offspring (Gowaty 1993, Komdeur 1996), species life history traits (Daan et al. 1996), and intrasexual competition for the nest site (Smallwood and Smallwood 1998) are among the most common hypotheses to explain the adaptiveness of biased sex ratios. In raptors, breeding parameters such as brood size, breeding success, and laying date may change according to food availability, population density, or weather conditions, showing great interannual and seasonal variation (Newton 1979, Kostrzewa and Kostrzewa 1990).

Although within season variation in sex ratio has been documented, interannual variation rarely has been considered in previous studies because long term data usually are lacking (Olsen and Cockburn 1991, Gowaty 1993, Weatherhead and Montgomerie 1995, Leroux and Bretagnolle 1996). We studied sex ratio variation of fledglings (tertiary sex ratio, *sensu* Smallwood and Smallwood 1998) in a population of American Kestrels from 1968 to 1997 in order to investigate interannual and intraseasonal variation in fledgling sex ratio. Furthermore, we compared the results from the Canadian and Florida populations to those from our Wisconsin population, which occurs at an intermediate latitude.

METHODS

We conducted the study in central Wisconsin (44° 13′ N, 89° 30′ W) in a 20,243-ha area. This area consists almost entirely of prairie and marshes with cultivated fields and woodlots. Each year from 1968 to 1997 we visited a mean of 50 (range 45–54) nest boxes provided specifically for kestrels about five times during the breeding season (range: 3–7; see Hamerstrom et al. 1973 for details). Young were sexed about one week before fledging on the basis of plumage (alar tract feathers; Smallwood and Smallwood 1998). We analyzed data on offspring sex ratio using only those

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TABLE 1. Models of the proportion of female fledglings in American Kestrel (*Falco sparverius*) broods as a function of year and of the laying date. Analyses are based on 265 broods (1,025 fledglings) in central Wisconsin, 1968–1997. The names 'laying date' or 'Laying Date' are models where the eight 15-day classes were considered as a factor or a continuous variable, respectively, and their interaction is noted 'x.' In model notation '+' indicates the absence of interaction and '·' when no effects were present, np = number of estimable parameters in the model, and AIC = deviance + 2 × np.

Model and notation	np	Deviance	AIC	AIC Diff	Rel Diff	AIC weights
1 Laying Date	2	305.7	309.7	0.0	188.4	0.877556
2 laying date	8	298.1	314.1	4.4	270.3	0.097236
3 ·	1	314.8	316.8	7.1	298.1	0.025207
4 Laying Date + year	29	280.0	338.0	28.3	289.4	6.28E-07
5 laying date + year	35	270.3	340.3	30.6	314.8	1.99E-07
6 year	28	289.4	345.4	35.7	305.7	1.55E-08
7 laying date × year	96	188.4	380.4	70.7	280.0	3.9E-16

nests for which all offspring were sexed and the clutch initiation date was known (for this reason the years 1986 and 1987 were excluded). We determined the clutch initiation date from the number of eggs in an incomplete clutch (this occurs in a large part of our dataset) or alternatively by backdating from the observed or inferred hatching date. The amount of error is negligible with respect to the 15-day date categories that we used. The proportion of female fledglings was modeled as a binomial variable using year and laying date as independent variables. Interannual variation was first investigated considering year as a random term in linear mixed models (procedure GLMM in GENSTAT 5.0 ver. 3.1; GENSTAT 5 Committee 1993), but the variance component was negative. We thus considered year as a fixed factor in generalized linear models in order to test an additive relationship between the two effects. Model selection followed the Akaike Information Criterion value (AIC; Burnham and Anderson 1998). This is the sum of the model deviance and twice the number of parameters in the model. We considered the model with the lowest AIC value to be the best compromise between description of the data (model deviance) and parameter used in the model. Finally, there were insufficient data to include brood size as a dependent variable in the model. Its influence on the pattern of offspring sex ratio was analyzed using chi-square analysis on pooled data (no year effect) as in Rosenfield et al. (1996). In this analysis we also included the broods for which clutch initiation dates were not known precisely (see above). For all analyses the significance level was set at $P \leq 0.05$.

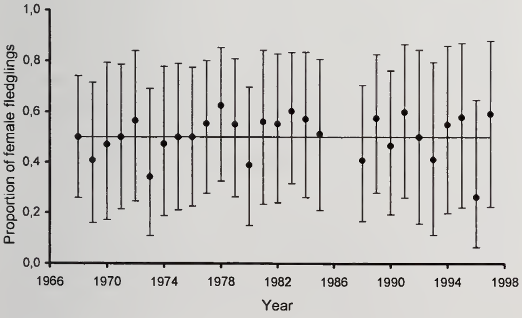

FIG. 1. Change in the proportion of female fledglings estimated from model 4 in Table 1. Analyses are based on 265 broods (1,025 fledglings) of American Kestrels (*Falco sparverius*) in central Wisconsin, 1968–1997. Bars indicate 95% confidence intervals. The horizontal line indicates the value of 0.5. Data from year 1986 and 1987 were excluded because laying date was not known precisely (see Methods).

RESULTS AND DISCUSSION

We modeled fledgling sex ratio in a total of 265 broods (1,025 fledglings) collected over 28 years (1968–1997) for which the first laying day was known. Afterwards, we determined that the extrabinomial variance was not significant ($X^2_{169} = 188.4$, $P = 0.15$), indicating that the effects of year, laying date, and their interaction provided a good description of the data in our model. We obtained a first important reduction in AIC value by dropping the interaction term (Table 1). A further reduction occurred when we did not consider the year effect (model 3 in Table 1). In contrast, the AIC value increased when the effect of laying date was dropped (model 4 in Table 1; Fig. 1). Indeed, the proportion of females on cumulated data was not significantly different from 0.5 (0.51, range: 0.48–0.54, from model 5) but seemed to increase with laying date. Modeling offspring sex ratio as a continuous linear function of the laying date provided a more parsimonious description of the data as indicated by the low AIC value of model 6 (Table 1). The regression model was

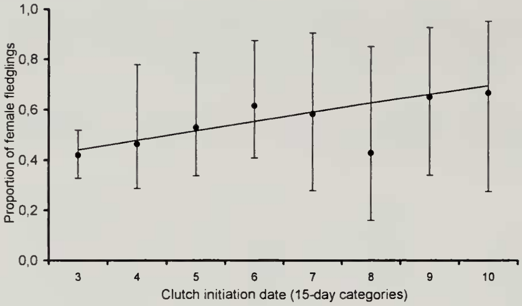

FIG. 2. Seasonal changes in the sex ratio in the American Kestrel (*Falco sparverius*) breeding in central Wisconsin, 1968–1997 (1,025 fledglings). The line indicates the values expected when the proportion of female fledglings is modeled as a continuous function of the laying date classes. Bars indicate 95% confidence intervals.

TABLE 2. Sex ratio by brood size of American Kestrels (*Falco sparverius*) in central Wisconsin, 1968–1997 (1,197 fledglings).

Brood size	Number of broods	Number of females	Number of males	% females
1	13	6	7	46.2
2	30	30	30	50.0
3	51	82	71	53.6
4	101	201	203	49.8
5	111	285	270	51.4
6	2	9	3	75.0
Total	308	613	584	51.2

$\text{logit}(f) = -0.69 + 0.15x \times L_{i,}$ where f is the proportion of female fledglings and L_i is the 15-day class i from 31 March (Fig. 2). Even in this more parsimonious environment (i.e., few effects are considered), the model assuming an additional effect of the year still was not retained (model 7 in Table 1). Finally, we detected no significant effect of brood size on fledgling sex ratio ($X^2_5 = 3.58$, $P = 0.61$; Table 2).

Sex biased mortality of nestlings may occur at different stages of the nesting period. The primary sex ratio is the sex ratio at fertilization, whereas a biased secondary sex ratio may occur through differential mortality of eggs. For example, Anderson et al. (1993) suggested that the observed sex-biased mortality of American Kestrel nestlings was due to the female chicks' competitive dominance over their male siblings. However, the sex of individual unhatched eggs was unknown and the sex of the young that did not fledge was not reported. Therefore, the mechanism by which these broods were biased is unknown. Nevertheless, we may consider alternative hypotheses for a male's fitness advantage of fledging early in the breeding season.

The Local Resource Competition Hypothesis (LRC) predicts that parents should produce a sex ratio biased in favor of the less competitive sex (Gowaty 1993, 1997). Therefore, LRC predicts that parents should bias their broods in favor of the sex that disperses farthest, but it cannot explain why sex ratio changes significantly during the breeding season.

An alternative hypothesis, proposed by Daan et al. (1996), to explain a seasonal shift in offspring sex ratio was based on size and sex specific differences in maturation time (age at first breeding). This Maturation Time Hypothesis (MTH) was modified from a general theory first proposed by Trivers and Willard (1973). For raptor species in which first breeding occurs early in life (e.g., the Eurasian Kestrel), the MTH predicts that early broods should be male biased because while all females start breeding at one year of age, only males from early clutches start at one year of age (Dijkstra et al. 1990). In contrast, raptor species with delayed maturation should have female biased broods. Thus, although the MTH explains differences in the pattern of the seasonal variation in sex ratio of some raptor species (Daan et al. 1996), it does not support the pattern shown by the American Kestrel in which males usually breed at one year of age (Del Hoyo et al. 1994). We do not know if age at first breeding varies latitudinally in American Kestrels. If so, then our findings might simply provide further support for the MTH.

However, the MTH does not consider the ecological conditions that confer sex specific advantages, such as availability of suitable nest sites (see Smallwood and Smallwood 1998). Smallwood and Smallwood (1998) proposed the Early Bird Hypothesis (EBH), suggesting that for nonmigratory populations that are nest site limited, early-fledged males are at a competitive advantage over later-fledged males since breeding territories are acquired during post-fledging dispersal (see also

Balgooyen 1976); no such advantage would occur in migratory populations, since territory acquisition occurs at the end of spring migration. Thus, the EBH accounts for the differences between the nonmigratory population studied in Florida and the migratory one studied in Canada, in which seasonal shift in sex ratio was not observed (Wiebe and Bortolotti 1992).

In the present study, we found evidence of a seasonal shift in sex ratio, despite the fact that our population is migratory. Because our study population in central Wisconsin is at an intermediate latitude relative to the Florida and Canada populations, we suggest that the seasonal sex ratio bias decreases from south to north. Three factors are consistent with this suggestion. First, our population is in the geographical limit of the migratory and nonmigratory areas (Del Hoyo et al. 1994). Second, the proportion of males does not vary greatly in our population (range: 0.41–0.53) compared to that of the Florida population (range: 0.36–0.58; Smallwood and Smallwood 1998). Third, in our study area the natural breeding sites (natural holes in large trees) were not abundant (only nine natural nests detected during 50 years of study; see also Hamerstrom et al. 1973) contrary to that observed in the study sites used by Wiebe and Bortolotti (Bortolotti and Iko 1992). Thus, there was considerable competition for suitable breeding sites.

In conclusion, our long term study supports the predictions of the EBH. Moreover this study suggests a latitudinal gradient of this effect may exist, as recently predicted by Pen et al. (1999) in a statistical model generated from an evolutionarily stable strategy approach to the brood sex ratio question.

ACKNOWLEDGMENTS

We thank all who helped with the fieldwork and F. Zugno for assistance on a previous version of the manuscript. We also thank J. P. Evans, A. Pilastro, and G. R. Bortolotti for editorial comments that improved the manuscript.

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